HISTORIC EXPANSION OF *JUNIPERUS OCCIDENTALIS* (WESTERN JUNIPER) IN SOUTHEASTERN OREGON

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ABSTRACT.—The chronology of *Juniperus occidentalis* (western juniper) expansion in eastern Oregon, the effect of plant canopy and interspace on *J. occidentalis* seedling establishment and growth rates, and the age of *J. occidentalis* maximum reproductive potential were determined. Measurements were recorded in twenty-two 0.4-ha plots established in sagebrush-grassland communities and six 0.1-ha plots in *Populus tremuloides* (quaking aspen) communities. *J. occidentalis* began increasing during the 1880s in stands containing trees >130 yr old. Relatively steady establishment ensued into the 1950s and then began to progress at a geometric rate in the 1960s. *J. occidentalis* encroachment into aspen stands began between 1910 and 1920. The largest proportion of juvenile trees established beneath *Artemisia* species in sagebrush-grassland communities. *J. occidentalis* trees appeared to reach full reproductive potential at >50 yr of age. The ratio of male:female trees increased from 1.7 in scattered *J. occidentalis* stands to 3.8 in closed stands. The initiation of *J. occidentalis* encroachment during the late 1800s coincides with optimal climatic conditions for *Juniperus* berry production and establishment, reduced fire-return intervals, and heavy livestock grazing. The accelerated increase in *J. occidentalis* expansion since 1960 may be due to the continued absence of fire, abundant woody plant cover, and the large increase in *J. occidentalis* seed production.

Key words: western juniper, Juniperus occidentalis, *expansion, Great Basin, intermountain shrub steppe, aspen,* Populus tremuloides, *succession.*

One of the most pronounced plant community changes in the 20th century has occurred in the juniper and pinyon-juniper woodlands, a major vegetation type characterizing the Intermountain Region. These woodlands, sometimes described as pygmy forests, currently occupy 17 million ha throughout this region (West 1988). *Juniperus occidentalis* ssp. *occidentalis* Hook. (western juniper) is considered the Northwest representative of the pinyon-juniper zone in the Intermountain Region (Franklin and Dyrness 1973) and occupies over 1 million ha (Dealy et al. 1978) in eastern Oregon, southwestern Idaho, and northeastern California (Cronquist et al. 1972). This subspecies of *J. occidentalis* is found primarily north of the polar front gradient (Neilson 1987; parallel to the Oregon and Nevada border, latitude 42°) where temperatures are cooler, summer precipitation decreases, and winter precipitation increases (Mitchell 1976).

Relict juniper woodlands, tree-age class distribution, fire scars, and historical documents indicate presettlement pinyon-juniper and juniper woodlands were usually open, savan-nah-like (Nichol 1937, West 1988), or confined to rocky surfaces or ridges (Cottam and Stewart 1940, Barney and Frishknecht 1974, Hopkins 1979, Johnson and Simon 1987). *J. occidentalis* began increasing in both density and distribution in the late 1800s (Burkhardt and Tisdale 1976, Young and Evans 1981, Eddleman 1987), invading *Artemisia tridentata* subsp. *vaseyana* (mountain big sagebrush), *Artemisia arbuscula* (low sagebrush), *Populus tremuloides* (quaking aspen), and riparian communities. Although *J. occidentalis* is long lived (Vasek 1966, Lanner 1984), less than 3% of the woodlands in Oregon are characterized by trees >100 years old (USDI-BLM 1990). In 1825, Ogden observed only occasional *J. occidentalis* (reported as cedars) growing on hillsides while traveling through the Crooked River drainage in central Oregon (Rich et al. 1950). Today, these hillsides are covered by dense *J. occidentalis* woodlands. In a nearby area J. W. Meldrum's 1870 survey notes describe a gently rolling landscape covered with an abundance of perennial bunchgrasses and a wide scattering of *J. occidentalis* trees (Caraher 1977). Today, *J.*

occidentalis densities on this site range between 125 and 250 ha⁻¹. In Silver Lake, Oregon, *J. occidentalis* density increased from 62 ha⁻¹ in 1890 to over 400 ha⁻¹ by 1970 (Adams 1975). On another site in central Oregon where trees were absent prior to 1880, *J. occidentalis* increased to 1018 ha⁻¹ by 1980 (Eddleman 1987). Recent expansion is similar to increases in other *Juniperus* species throughout western United States (Ellis and Schuster 1968, Tausch et al. 1981, West 1984, Tausch and West 1988).

The objectives of our study were to (1) describe the chronology of *J. occidentalis* expansion during the past several centuries in southeastern Oregon, (2) determine the effect of plant canopy and interspace on *J. occidentalis* seedling establishment and growth rates, and (3) determine the age when *J. occidentalis* reaches maximum reproductive potential.

METHODS

Study Area

The study area is located on Steens Mountain in southeastern Oregon, approximately 80 km south of Burns. This isolated volcanic fault-block, which lies in the extreme northwest Basin and Range Province (Fenneman 1931), is about 80 km long and oriented in a northeast direction (Baldwin 1981). The elevation of Steens Mountain ranges from 1268 to 2949 m, with a steep east-facing escarpment and a gentle west-facing slope. Climate is cool and semiarid, characteristic of the northern Great Basin. Annual precipitation at the lower elevations averages 220–280 mm, increasing to ≥ 700 mm at higher elevations (NOAA 1993). Most moisture is received as snow in November, December, and January and as rain in March through June.

J. occidentalis woodlands on Steens Mountain form a discontinuous belt between 1450 and 2100 m in elevation. Severe winter conditions probably restrict *J. occidentalis* from expanding into higher elevations (Billings 1954, Mehringer 1987). Limited distribution below 1500 m is possibly due to a combination of late spring frosts (Billings 1954) and limiting moisture. Tree canopy cover varies from open to 30% cover, except on mesic *P. tremuloides* sites where *J. occidentalis* cover approaches 100%. However, based on age structure and canopy leader growth, tree canopies are still actively expanding on the majority of sites measured. Early observations on Steens Mountain indicate the landscape contained only scattered stands of *J. occidentalis* (Griffiths 1902). Since 1900 the abundance of *J. occidentalis* pollen in the Steens Mountain area has increased five-fold (Mehringer and Wigand 1990).

Plant communities characteristic of *J. occidentalis* woodlands are *Artemisia tridentata* ssp. *vaseyana*/*Festuca idahoensis* (Idaho fescue), *Artemisia arbuscula*/*F. idahoensis*, and *P. tremuloides*. *P. tremuloides* communities on Steens Mountain range in elevation from 1760 to 2400 m. At lower elevations, in the *J. occidentalis* woodland belt, *P. tremuloides* stands form long, narrow communities along north aspects, which capture windblown snow and runoff.

Plot Layout

Plot locations were selected in an attempt to reflect sagebrush-grassland communities in different stages of *J. occidentalis* invasion on the west slope of Steens Mountain. Old stands on the rocky outcrops, which make up only a small percentage of present-day woodlands, were not measured. Sites selected support, or have the potential to support, sagebrush-grassland communities. Currently these sites are occupied by varying numbers and sizes of *J. occidentalis* dominance, creating a woodland structure of dispersed, intermediate, and closed tree stands (Table 1). Twenty-two 0.4-ha plots were located within the *J. occidentalis* belt of Steens Mountain; they ranged from 1500 to 2000 m in elevation and were distributed 32 km along the mountain range. Plots were situated along an elevation gradient representing communities from the lower- to upper-elevation *J. occidentalis* woodland belt. Dominant understory vegetation in the dispersed and intermediate plots was *A. tridentata* spp. *vaseyana* and *Festuca idahoensis* (13 stands), *A. arbuscula* and *F. idahoensis* (4 stands), and a mosaic of *A. arbuscula* and *A. tridentata* ssp. *vaseyana* (2 stands). Understory vegetation in the closed stands ($n = 3$) comprised a few remnant deep-rooted perennial grasses, skeletons of dead *A. tridentata* ssp. *vaseyana*, and 70% bare ground (EOARC data file).

An additional six 0.1-ha plots were established in six separate *P. tremuloides* stands. Three stands were in advanced stages of *J. occidentalis* invasion with few to no adult *P.*

TABLE I. *Juniperus occidentalis* stand maturity classes in *Artemisia* communities (modified from Blackburn and Tueller 1970).

Closed	Abundant adult trees generally >5 m tall and usually several trees >130 yr of age, with little understory, particularly on south slopes.
Intermediate	Abundant *J. occidentalis* of all age classes, with a more open tree canopy and an understory beginning to decline; trees >130 yr of age are rare.
Dispersed	Abundant young trees <2 m tall, a few adult trees but old trees absent, and a well-developed understory.

tremuloides trees and dead *P. tremuloides* trunks on the ground. The remaining three stands were characterized by a dominant *P. tremuloides* overstory and an understory of young *J. occidentalis*. Elevation for the *J. occidentalis*–*P. tremuloides* plots ranged from 1930 to 2000 m, all with a similar northeast aspect.

Measurements

Prior to sampling, string was stretched along the contour of each 0.4-ha plot at 1-m intervals to keep track of measured trees. *J. occidentalis* density (trees ha^{-1}) was recorded for trees <0.5 m tall, defined as adult, across the entire plot. Tree height, minimal and maximal crown diameters, and basal area just above the trunk swell at the stem base near the litter layer were recorded. Tree height was measured with a tape for trees ≤ 2 m and a clinometer for trees >2 m tall. Tree canopy cover was estimated by adding crown area measurements of all trees for each plot. Similar measurements were recorded on juvenile trees (defined as trees ≤ 0.5 m tall), but only those on the lower left quarter (0.1 ha) of each 0.4-ha plot. Current-year *J. occidentalis* seedlings (any plant with cotyledons still attached) were not recorded. Establishment location of each juvenile tree was recorded: beneath the canopy of *J. occidentalis*, *Artemisia*, other shrubs, tussock grass, or in the interspace. Less than 1% of juveniles were located beneath other shrubs or grasses; therefore, only *J. occidentalis*, *Artemisia*, and interspace are reported.

J. occidentalis is considered submonoecious (Vasek 1966). Male and female reproductive status was determined by estimating abundance of cones and berries for each tree. Abundance was ranked in four classes: (0) absent, (1) scarce,

(2) obvious but not abundant, and (3) abundant.

In each plot a 10-tree subsample was randomly selected for aging in each of four height classes: (1) <0.5 m, (2) 0.5–1.8 m, (3) 1.8–3 m, and (4) >3 m. In several of the dispersed plots, sample size for trees >3 m was smaller than 10, due to a lack of trees. We also sampled all old trees on plots when they occurred (n = 0–5 ha^{-1}). Old trees were easily identified by their growth form, containing rounded tops and heavy limbs, and lacking strong terminal leader growth (Burkhardt and Tisdale 1969). A cross section was removed approximately 30 cm above ground level from each tree >0.5 m tall and at ground level for trees ≤ 0.5 m, and then brought back to the lab for aging. Two radii from each cross section were polished, stained, and counted. Age was estimated by averaging both radii and adding 10 yr to correct for the 30-cm base. Mean differences between radii were 4% for trees >50 yr and 1% for trees ≤ 50 yr of age. Adams (1975) reported that growth-ring characteristics of *J. occidentalis* are useful in dendrochronological studies. The presence of false and missing rings was similar to that for *Pinus ponderosa*. Over 1200 trees were aged and approximately 14,000 counted and measured. In the six *P. tremuloides* stands, density of both *J. occidentalis* and *P. tremuloides* and age and height for *J. occidentalis* were measured across the entire 0.1-ha plot.

Evidence indicated minimal *J. occidentalis* mortality has occurred on Steens Mountain during the past 120 years. We observed very few dead or dying trees for all age classes (excluding seedlings), except where individual *J. occidentalis* trees had been cut or burned. Mortality of *Juniperus* species rapidly declines following the seedling stage (Van Pelt et al. 1990). *Juniperus* has few pests that prove fatal to the tree (Lanner 1984). We avoided recently cut or burned stands, which constituted a small percentage of *J. occidentalis*–occupied stands. Where remains of dead trees were observed, we noted they persisted for a long period of time. By recutting several stumps adjacent to one of our plots and aging and matching ring widths with adjacent live trees, we determined these trees were harvested around 1920. Others have also observed the persistence of *Juniperus* stumps (Young and Budy 1979).

Statistical Analysis

Height growth data for adult trees were analyzed using a randomized complete block design in PROC GLM of SAS (SAS 1986). Means were separated using Duncan's Multiple Range Test at $p \leq .05$ level. A split-plot design was used in the analysis of juvenile height growth. Main plots were sites and sub-plots were location of establishment (interspace, *Artemisia*, *J. occidentalis*). A Duncan's Multiple Range Test was used to separate the means.

RESULTS

Little change in *J. occidentalis* density appeared to occur between the early 1700s and the 1880s (Fig. 1). We encountered old trees (standing trees >130 years old, large stumps, and burned-out trunks) on several *A. arbuscula* flats and *A. tridentata* ssp. *vaseyana* communities. However, data indicated presettlement tree densities in these *Artemisia* communities were ≤ 5 trees ha^{-1}, suggesting very open *J. occidentalis* stands. The first evidence of an increase in tree densities occurred in the 1880s, with relatively steady establishment ensuing into the 1950s, similar to that observed by Tausch and West (1988). In the 1960s *J. occidentalis* establishment began occurring at a geometric rate.

Closed *J. occidentalis* stands, which once supported *A. tridentata* ssp. *vaseyana*, were characterized by an abundance of adult trees (≥ 3 m tall), a tree canopy cover of 18–28% (Table 2), and the presence of a few old trees (130+ yr; 2 to 5 ha^{-1}). *J. occidentalis* densities began increasing in these stands between 1878 and 1890. In the intermediate *J. occidentalis* stands, trees >130 yr were rare. Tree canopy cover ranged from about 8 to 16%, and densities of adult trees varied from 35 to 100 ha^{-1}. Trees <3 m in height, particularly juveniles, were abundant. *J. occidentalis* expansion in these sagebrush-grassland communities began between 1890 and 1910. In the dispersed stands few trees were >60 yrs old, and we aged no trees >100 yr. Tree canopy cover was usually <5% in the dispersed stands and densities of large adult trees <35 ha^{-1}. Invasion of *J. occidentalis* into these sagebrush-grassland communities began after 1930.

Greatest densities of *J. occidentalis* trees measured on Steens Mountain occurred in *P. tremuloides* sites (Table 3). In the late stages of *J. occidentalis* succession on these sites, tree canopy cover approached 100%. Live *P. tremuloides* occurred only on one of the three sites, and almost all trees were <0.5 m tall. In the remaining two stands only the remnants of large *P. tremuloides* trunks decaying in the understory were present. *J. occidentalis* invasion in these *P. tremuloides* sites began between 1910 and 1920. No *J. occidentalis* trees
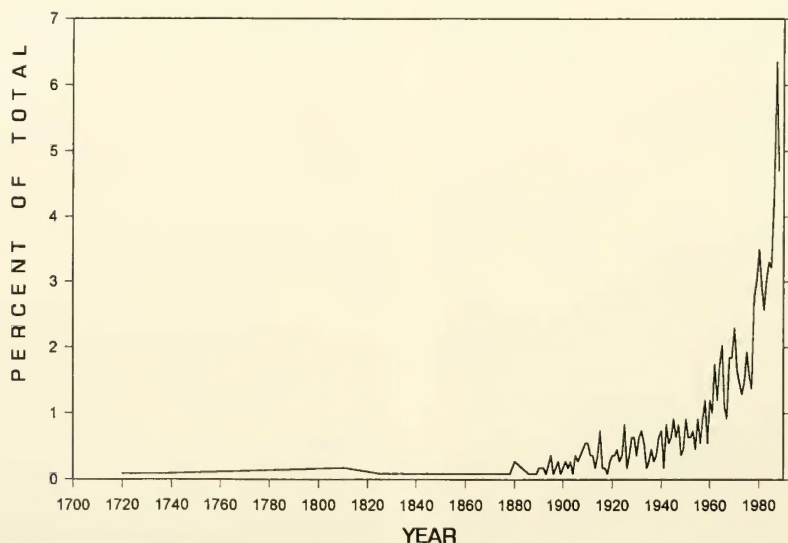

Fig. 1. Years of establishment for *Juniperus occidentalis* trees on Steens Mountain, Oregon ($n = 1200$).

TABLE 2. General description of closed, intermediate, and dispersed *Juniperus occidentalis* stands on Steens Mountain in *Artemisia tridentata* ssp. *vaseyana* and *A. arbuscula* communities, and the percentage of juveniles located beneath *J. occidentalis*, *Artemisia*, and interspace. Canopy cover, basal area, and density means are followed by range in parentheses ( ).

	# sites	Canopy cover %	Basal area (m²ha⁻¹)	Density (#ha⁻¹) Adults >0.5 m ht	Density (#ha⁻¹) Juveniles <0.5 m ht	Establishment site % (for juveniles) *J. occidentalis*	Establishment site % (for juveniles) *Artemisia*	Establishment site % (for juveniles) Interspace
A. tridentata ssp. *vaseyana*								
closed	6	22 (18–28)	5.2 (3.1–9.8)	296 (217–496)	580 (118–1226)	86[a1]	9[b]	5[b]
intermediate	8	6 (5–10)	1.8 (0.5–4.7)	95 (50–165)	815 (335–1423)	29[b]	58[a]	13[c]
dispersed	2	2 (1–3)	0.4 (0.2–0.6)	52 (31–70)	188 (96–280)	3[b]	50[a]	47[a]
A. arbuscula								
closed	3	15 (12–20)	3.5 (1.8–5.4)	158 (74–247)	99 (20–198)	27[b]	67[a]	6[c]
intermediate	3	6 (4.5–6.7)	1.8 (0.9–3.2)	104 (77–153)	375 (167–790)	11[b]	61[a]	28[b]

[1]Sites of establishment means (%) followed by similar lowercase letters are not significantly different between establishment sites within *J. occidentalis* stand maturity classes ($p \leq .05$).

>80 yr were encountered. In stands with a *P. tremuloides* overstory, *P. tremuloides* density of small shoots was greater than that of *J. occidentalis*. However, *P. tremuloides* size classes between 0.5 m and large adults were absent, indicating a lack of *P. tremuloides* stand rejuvenation. On these sites *J. occidentalis* invasion began between 1930 and 1940.

Height growth for young *J. occidentalis* trees (<20 yr) across all sites averaged 2.9 cm yr⁻¹. Based on growth rates and height of trees between 10 and 20 yr of age ($n = 200$) across all *Artemisia* sites, 90% of trees 15 yr old were <1 m tall (64% were <0.5 m tall). Surprisingly, height growth rates of juvenile trees did not significantly differ between *A. arbuscula* and *A. tridentata* ssp. *vaseyana* communities. However, location of establishment within communities significantly influenced growth rates of young *J. occidentalis* trees (Table 4). Trees establishing beneath an *Artemisia* canopy grew faster than young trees growing in the interspace.

Shrub and tree canopies also significantly influenced location of *J. occidentalis* seedling establishment in *Artemisia* communities. The largest proportion of juvenile trees was usually located beneath canopies of *A. tridentata* ssp. *vaseyana* or *A. arbuscula* and *J. occidentalis* (Table 2). Less than 20% of juveniles across all 22 *Artemisia* sites established in the interspace.

On Steens Mountain, for trees >0.5 m tall, 32% expressed predominantly only male or only female characteristics, 38% both male and female, and 30% contained neither fruits nor cones. *J. occidentalis* trees producing abundant crops of cones or berries were either male or female dominant. No trees were measured which contained an abundant crop of both berries and cones. Sixty-five percent of *J. occidentalis* trees with an abundant crop of berries contained no male cones. The remaining 35% contained only a scarce number of cones. The majority of trees producing abundant crops of male cones contained only scarce numbers of berries. Approximately 75% of trees producing heavy crops of berries or cones were >50 yr old. Trees <20 yr old expressing reproductive effort were rare and produced only a few cones or berries. The ratio of trees producing large crops of cones versus berries (cones:berries) increased from 1.7 in the scattered *J. occidentalis* stands to 3.8 in the closed stands.

DISCUSSION

Low densities and limited distribution of *J. occidentalis* trees >130 yr and limited numbers of dead trees or old stumps suggest *J. occidentalis* has greatly expanded on Steens Mountain during the past 100 yr. Distribution of old trees was generally limited to rocky ridges and *A. arbuscula* communities. Old trees were found only occasionally growing in deeper, well-drained soils such as *A. tridentata* ssp. *vaseyana* grassland communities and were absent in *P. tremuloides* communities. In northeastern California, Barbour and Major

TABLE 3. Mean densities (# ha⁻¹) followed by range in ( ) of *Populus tremuloides* and *Juniperus occidentalis* in *P. tremuloides* sites.

Stage of succession	P. tremuloides		J. occidentalis	
	Adult	Juvenile	Adult	Juvenile
Late (n = 3)	17 (0–50)	1316 (0–3952)	1392 (929–2203)	9462 (4327–18,791)
Intermediate (n = 3)	1060 (476–1670)	6553 (5266–9480)	1090 (632–1739)	2816 (622–5968)

(1977) found a similar distribution of old and young *J. occidentalis* trees. *A. tridentata* ssp. *vaseyana* and *A. arbuscula* communities, which contained a low density of *J. occidentalis* trees prior to settlement, were the earliest sites to initiate an increase in *J. occidentalis*. Dates of initial establishment of closed and intermediate stands were similar to periods of early stand development reported by Young and Evans (1981) in northeastern California and Eddleman (1987) in central Oregon.

Expansion of *J. occidentalis* coincides with Euro-American settlement in this portion of the Great Basin. Although no direct cause-and-effect relationship can be drawn, we hypothesize that climate, altered fire frequencies, and grazing in the late 1800s were primary factors initiating the recent expansion of *J. occidentalis*. Following the end of the Little Ice Age in the mid 1800s (Bryson 1989), winters became more mild and precipitation increased above the present long-term average in the northern half of the Great Basin between 1850 and 1916 (Antevs 1948, Graumlich 1985). Mild, wet winters and cool, wet springs promote vigorous growth in *J. occidentalis* (Earle and Fritts 1986, Fritts and Xiangdig 1986).

Presettlement fire-return intervals in *A. tridentata* ssp. *vaseyana* communities have been reported to vary from 15 to 25 yr (Houston 1973, Burkhardt and Tisdale 1976, Martin and Johnson 1979). Burkhardt and Tisdale (1976) concluded that fire-frequency intervals of 30–40 yr would be adequate to keep *J. occidentalis* from invading a sagebrush-grassland community. Following settlement, frequency of fire in sagebrush grasslands has greatly declined. The reduction of fine fuels by high densities of domestic livestock greatly reduced the potential for fire in the Intermountian Shrub Region (Burkhardt and Tisdale 1976, West 1988). Griffiths' (1902) observations of the overgrazed landscape on Steens Mountain

support this hypothesis. Fires set by Native Americans also declined in the 19th century due to large reductions in their populations caused by European diseases (Thompson 1916, Cressman 1981) and relocation to reservations in the 1870s.

The invasion of conifers into *P. tremuloides* communities is a common occurrence throughout the western U.S. However, conifers reported to typically invade *P. tremuloides* stands are species adapted to more mesic sites such as *Pinus contorta* (lodgepole pine), *P. ponderosa*, *Pseudotsuga menziesii* (Douglas-fir), *Abies concolor* (white fir), *Abies lasiocarpa* (subalpine fir), *Picea engelmannii* (Engelmann spruce), and *Picea pungens* (blue spruce) (Bartos 1973, Mueggler 1985). Invasion of the more drought-tolerant *J. occidentalis* into *P. tremuloides* stands is not well documented.

P. tremuloides is frequently considered a fire-induced species, replaced by less fire tolerant conifers (Baker 1925, Daubenmire 1943, Mueggler 1976). Prior to settlement, lightning and human-set fires probably helped maintain many *P. tremuloides* communities. However, the occurrence of fire in *P. tremuloides* stands in the Rocky Mountains has been greatly reduced since the late 1800s (Jones and DeByle 1985). Mueggler (1985) suggested the combination of fire suppression and heavy grazing in *P. tremuloides* communities may favor the establishment of conifers.

An increase in *Artemisia* cover may also enhance the invasion of *J. occidentalis*. As a sagebrush-grassland community shifts towards a greater dominance of shrubs, the number of safe sites for *J. occidentalis* seedling establishment increases. Others have also reported the majority of *J. occidentalis* seedlings established beneath *Artemisia* canopies (Burkhardt and Tisdale 1976, Eddleman 1987). In west Texas, *J. pinchotii* frequently establishes beneath mesquite plants (McPherson et al. 1988).

TABLE 4. Mean growth rates for juvenile *Juniperus occidentalis* trees (2–30 yr old) in three different establishment sites.

Establishment site	cm yr^{-1}
Artemisia	3.3[A]
J. occidentalis	2.7[AB]
Interspace	2.4[B]

Means followed by similar uppercase letters are not significantly different ($p \leq .05$).

Shading by nurse plants may benefit *J. occidentalis* seedlings (Johnsen 1962) by reducing summer surface temperatures by 45–57% of bare ground surface temperatures (Burkhardt and Tisdale 1976). Enhanced growth rates of young trees growing beneath *A. tridentata* ssp. *vaseyana* suggest microclimates beneath shrub canopies are more beneficial than conditions in the interspace. Burkhardt and Tisdale (1976) reported *J. occidentalis* seedling growth rates were correlated positively with *Artemisia* and correlated negatively with bare ground.

J. occidentalis approached full reproductive potential near 50 yr. As *J. occidentalis* densities increased, the proportion of trees became predominantly male across sites. Highly fecund female trees appeared to be most important in open stands where *J. occidentalis* was actively expanding. In central Oregon, Eddleman (1984) observed that trees in the interior woodlands were strongly dominated by male cone production while trees growing in the open produced more female cones. He also reported trees did not produce significant quantities of fruit until 50–70 yr of age.

Conclusion

Optimal climatic conditions around the turn of the century, reduced fire return intervals, and the indirect effect of livestock through the reduction of fine fuels and an increase in *Artemisia* cover are probably primary factors that have contributed to the rapid expansion of *J. occidentalis* in southeast Oregon during the late 1800s and early 1900s. The accelerated increase in *J. occidentalis* density and invasion during the last 30 years into new communities is probably largely due to the continued absence of fire, abundant woody plant cover, and the large increase in *J. occidentalis* seed rain.

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